

Review of the genus *Hyrtanella* (Ephemeroptera: Ephemerellidae)

LUKE M. JACOBUS¹ & MICHEL SARTORI²

¹Department of Entomology, Purdue University, West Lafayette, Indiana 47907, USA
E-mail: luke_jacobus@entm.purdue.edu

²Musée cantonal de zoologie, CP 448, CH-1000 Lausanne 17, Switzerland

ABSTRACT

The genus *Hyrtanella* Allen and Edmunds (Ephemeroptera: Ephemerellidae) is distinguished from other Ephemerellinae by larvae that have fully operculate gills and single median spines on the posterior margins of abdominal terga 8 and 9. Eggs have one polar cap and a smooth chorion. Male adults are not known, and female alates cannot be assigned to species, based on present data. The genus probably is endemic to the island of Borneo, and it contains two species: *H. christineae* and *H. pascalae*, new species. *Hyrtanella pascalae* is described based on eggs, larvae, and one male subimago. The larva of *H. pascalae* is distinguished from *H. christineae* by its smaller size, blunt genal projections, and smooth forefemora. The male subimago has genital forceps segment 3 elongate.

KEY WORDS: *Hyrtanella*, Ephemeroptera, Ephemerellidae, Ephemerellinae, *Hyrtanella christineae*, *Hyrtanella pascalae*, new species, descriptions, Borneo, misidentifications

INTRODUCTION

The genus *Hyrtanella* Allen and Edmunds (Ephemeroptera: Ephemerellidae) was described for some distinctive larvae and female adults from the island of Borneo (Allen & Edmunds 1976). The monospecific genus (type species: *H. christineae* Allen and Edmunds) has been classified in the monogeneric tribe Hyrtanellini (Allen 1980; Allen 1984) of the subfamily Ephemerellinae (McCafferty & Wang 2000). Landa *et al.* (1982) and Landa and Soldán (1985) provided details about the internal anatomy of *Hyrtanella*.

Edmunds and Polhemus (1990) reported the genus from the Malay Peninsula, northern Thailand, and southern India, but these records probably are based on misidentifications.

Records of the genus *Hyrtanella* from outside Borneo (Edmunds & Polhemus 1990) are based only on female alates. The specimens on which these records are based are morphologically different from the female adults of *Hyrtanella* that were described by Allen and Edmunds (1976). Specimens that have been identified as *Hyrtanella*, but which are from outside the island of Borneo [e.g., 10 female alates (eggs removed from one specimen) from the Malay Peninsula, Malaysia (west), Selangor, large trib Sungai Selangor (24°C), 6 mi NE Kota Kuba Baharu (Mile 44), 1/IX/1978, collected by G. F. and C. H. Edmunds, deposited in Purdue University Entomological Research Collection], do not have abdomens with enlarged posterior segments, a medial constriction (possibly a sexual difference in *Hyrtanella*), or blunt spines on the posterior terga. Furthermore, the ultrastructure of eggs (Fig. 20) extracted from this material is different from that of *Hyrtanella* (Fig. 19), but it is similar to that of species from several other genera, including *Serratella* Edmunds, *Torleya* Lestage, and *Uracanthella* Belov (Okazaki 1984; Kang & Yang 1995; Studemann & Landolt 1997; Jacobus *et al.* 2004). Most likely, the specimens in question belong to *Torleya* or *Crinitella* Allen and Edmunds. Female alates of *Crinitella* and certain Oriental *Torleya* might be misidentified as *Hyrtanella*, based on size and wing coloration details, which we extrapolated from descriptions and discussions of larvae given by Wang and Sites (1999), Jacobus and McCafferty (2003), and Jacobus *et al.* (2004).

Although *H. christineae* is the only species that has been described in the genus *Hyrtanella*, Allen and Edmunds (1976) reported, but did not name or describe, a *Hyrtanella* species from Kuala Lumpur, Malaysia, that was contained in the collection of John E. Bishop. Janice G. Peters (Tallahassee, Florida) kindly loaned to us Ephemerellidae collected as part of Bishop's (1973) study of the Sungai Gombak. We did not locate any *Hyrtanella* species in this collection.

Recently, Sartori *et al.* (2003) provided additional reports of the genus *Hyrtanella* from Borneo. The specimens on which these reports are based represent a new species of *Hyrtanella*, which we describe and discuss below. The holotype and most of the paratypes are deposited at the Musée de Zoologie, Lausanne, Switzerland [MZL], and additional paratypes and other materials are deposited in the Purdue University Entomological Research Collection, West Lafayette, Indiana, USA [PERC], Florida A & M University, Tallahassee, Florida, USA [FAMU], The Natural History Museum, London, England [BMNH], and the Museum of Zoology, Indonesian Institute of Sciences, Jakarta Bogor, Indonesia [LIPI].

***Hyrtanella* Allen and Edmunds**

Diagnosis. *Larvae* are distinguished by having claws with basal denticles and a set of long subapical denticles; gills 3 operculate, with a median, transverse, weakened band; paired, blunt spines on abdominal terga 4–7; single, median spines on abdominal terga 8 and 9; and abdominal segments 8 and 9 reduced in width (Allen & Edmunds 1976).

Female adults are distinguished by having a reduced number of marginal intercalaries between CuA and IMP in the forewing (one intercalary between IMP and MP₂, and no intercalaries between MP₂ and CuA), a relatively small hindwing with few crossveins and a sharp costal projection, a constricted abdomen, a medial spine vestige on abdominal segment 8, and enlarged abdominal segments 8 and 9 (Allen & Edmunds 1976; Allen 1980).

Discussion. In the original description, Allen and Edmunds (1976) erroneously described gills present only on segments 3–6. As noted by McCafferty and Wang (2000) and Kluge (2004), *Hyrtanella* larvae indeed possess gills on segments 3–7.

Hyrtanella christineae Allen and Edmunds

Fig. 9

Diagnosis. *Larvae* (Allen & Edmunds 1976: Figs. 1, 5, 6) have sharp genal and frontal spines that are upturned; the third segment of the labial palp relatively wide proximally; the mandibular base produced into a lateral protuberance; prominent, bluntly pointed projections on the upper surface of the forefemur; and prominent, paired, bluntly pointed projections on the thoracic and abdominal sterna.

Larval variability. Allen and Edmunds (1976) described *H. christineae* as having a body length of 6.5–7.5 mm. However, we examined some final instar *H. christineae* specimens with a body length of up to 9.5 mm. One larva from the Liwagu River, north of Kundassan, has two more dorsal projections on the thorax than described by Allen and Edmunds (1976).

Discussion. The series of paratype larvae that we examined includes early, middle, and late instars.

Material examined. Island of Borneo—MALAYSIA (east), **Sabah:** Liwagu R, N of Kundassan, 915m elev., S8e, 16–17/VIII/1972, GF&CH Edmunds, two larvae [PERC]; Liwagu R, Liwagu Cave, SE of Headquarters, 1525m elev., S7e, 14–15/VIII/1972, GF&CH Edmunds, 24 larvae (paratypes) [PERC]; same data, six larvae [MZL, PERC]; Silau-Silau Stream, N of Kinabalu NP Headquarters, 1585m elev., S3e, 11/VIII/1972, GF&CH Edmunds, one larva [PERC].

Hyrtanella pascalae, new species

Figs. 1–8, 10–19

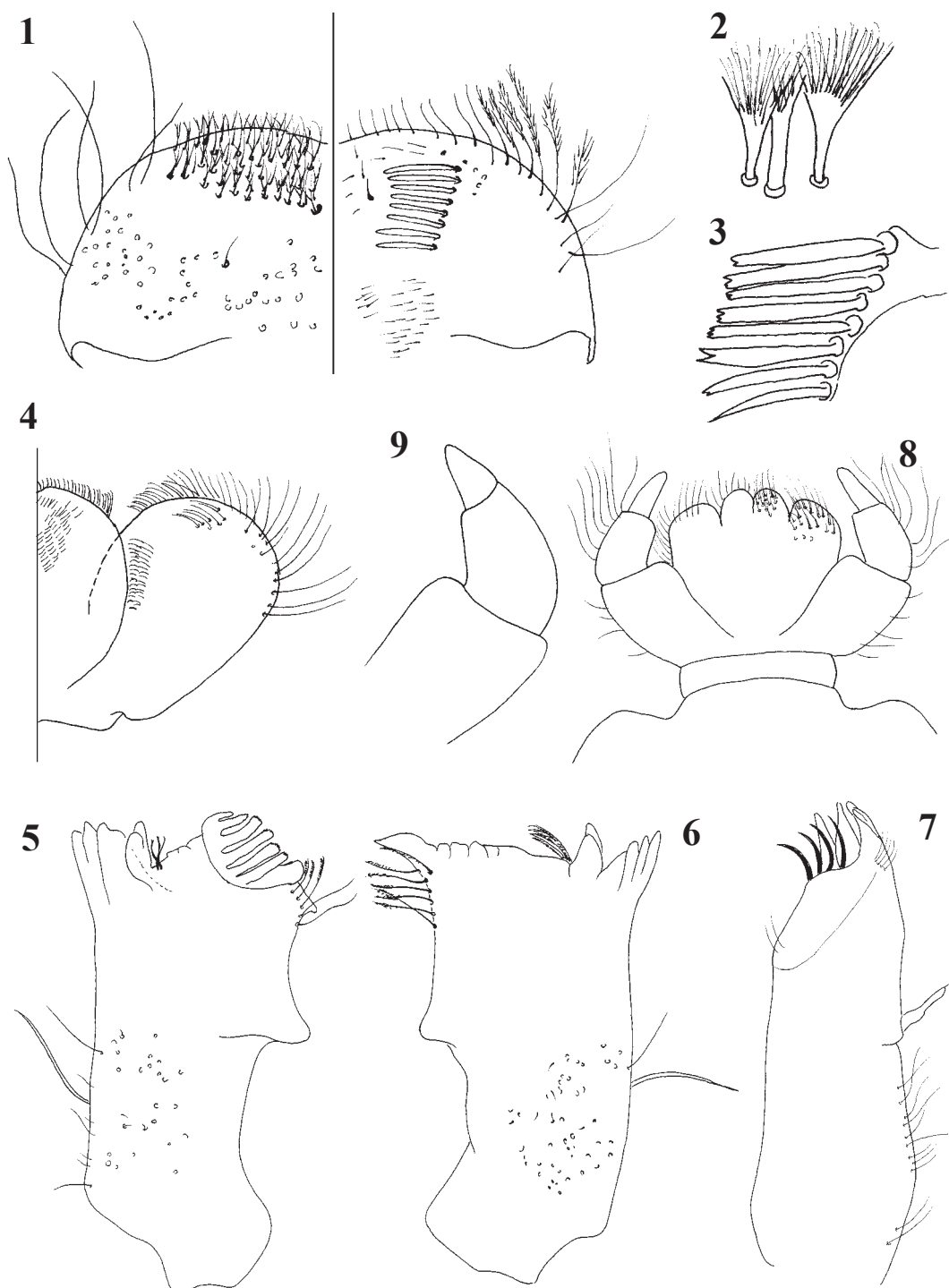
Descriptions. *Larva* (Figs. 1–8, 10–14)—Length: body 4.0–4.4 mm; caudal filaments 1.4–2.1 mm. Body color light brown.

Head: vertex with two pairs of short suboccipital spines. No ocellar bumps. Inner margin of antennal base with short projections. Frontal shelf not expanded. Genae slightly produced. Long hairlike setae present along anterior margin of frontal shelf and sparsely

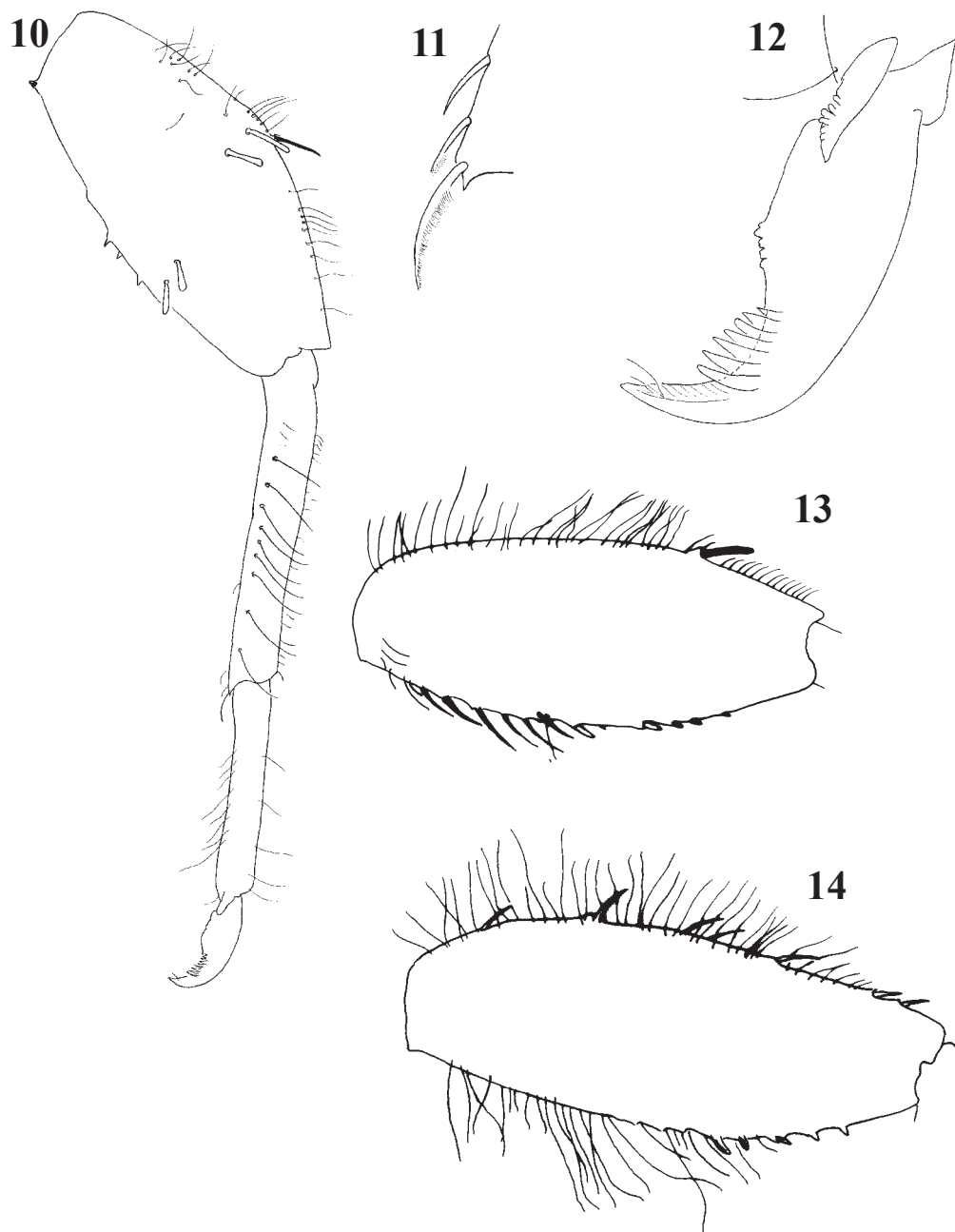
present below compound eye. Clypeus with anterior row of long hairlike setae. Labrum (Fig. 1) width nearly 2x length, with shallow, very broad notch anteriorly; dorsal face with scattered long hairlike setae on lateral margin and with several rows of brushlike setae anteriorly (Fig. 2); ventral face with simple or fimbriate setae on lateral margins and dense transverse row of 7–9 long, stout setae (Fig. 3). Hypopharynx with superlinguae size nearly subequal to linguae size (Fig. 4); lingua with row of short setae on anterior margin; superlingua with row of long, thin setae on margin, with setae decreasing in length anteriorly. Mandibles (Figs. 5, 6) with lateral setae relatively long. Maxilla (Fig. 7) with palp reduced; apex of galea relatively sharp with 3 incisors, and with no setae distally on outer margin; lacinia with 2 stout spinous processes (dentisetae) and with double row of 4 stout setae. Labium (Fig. 8) reduced; palp segments short; terminal segment length about 3 times basal width.

Thorax: Prothorax width subequal to head width, with no anterolateral projections and no dorsal spines; anterior margin upturned and not receded; ventral spines absent. Mesonotum with forewingpads base darkly pigmented and no spine between forewingpads. Coxae with slight dorsolateral projections; projections with hairlike setae. Legs with marginal long hairlike setae; femora generally flattened. Forefemur (Fig. 10) with incomplete narrow transverse band of dorsally projecting bristlelike setae; dorsal edge with single stout bristlelike seta medially; ventral edge with few chalazae medially; anterior face with no dorsal projections; foretibial projection short (Fig. 11). Claws bent, with short subdistal setae; palisade of elongate denticles on inner distolateral margin and few denticles present proximally (Fig. 12). Dorsal edge of midfemur (Fig. 13) with single stout bristlelike seta, but seta situated more distally than similar seta of forefemora; ventral edge with numerous chalazae, with proximal chalazae bearing long, bristlelike setae and distal chalazae with blunt, stout setae. Dorsal edge of hindfemur (Fig. 14) with 6–8 chalazae bearing long, bristlelike setae; ventral edge with only blunt and stout chalazae on distal half.

Abdomen: Gills similar to those of *H. christineae* (see Kluge 2004: Figs. 94a–e). Gills 3 brown with no apparent distal pigmentation; gills 4–7 translucent. Gills 3 operculate, with medial transverse weak band; gills 4 operculate. Dorsal lamellae of gills 4–6 with strong projection on inner proximal margin; projection folded dorsally; gills with slight projection on outer proximal margin. Dorsal lamellae truncate apically. Gills 3–6 ventral lamellae bifid, with dorsal and ventral lobules; lobules tips acute. Gills 7 narrow; point of attachment medial. Terga 1 and 2 with long hairlike setae on posterior margins. Terga 3–7 or 4–7 with pair of blunt oblique ridges and with short, blunt, paired spines on posterior margins; spines and ridges form inner portion of prominent gill chamber. Tergum 8 sculpted posterolaterally, and with single, short, blunt, median spine and blunt posterolateral projections. Tergum 9 with single, short, blunt, median spine and weak oblique ridges. Segments 6–8 with lateral margins strongly upturned, forming outer portion of prominent gill chamber. Abdominal sterna flattened, with no maculation and no long setae. Caudal filaments pale, with dense whorls of long hairlike setae.

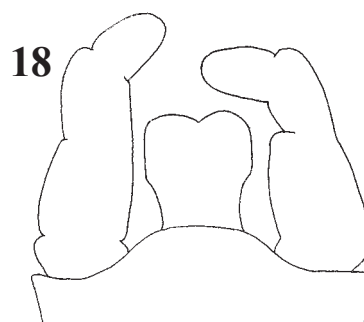
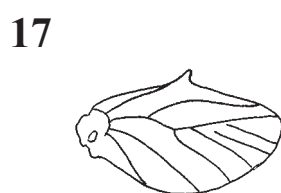
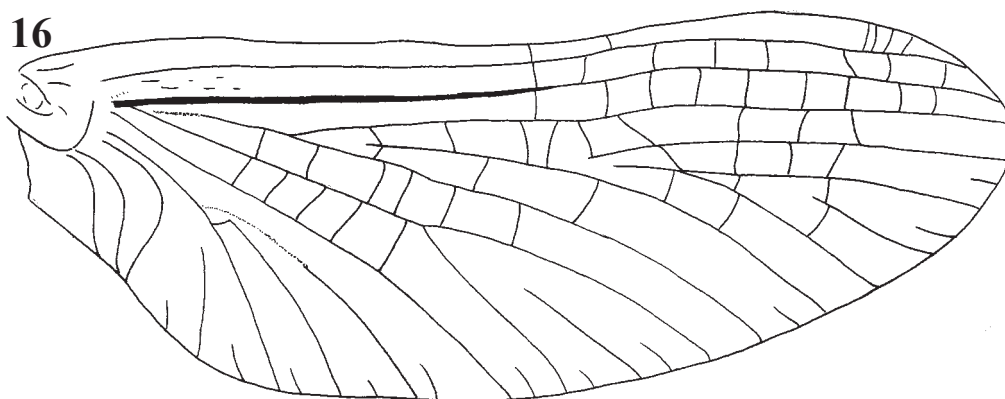


FIGURES 1–9. Figs 1–8. *Hyrtanella pascalae*, n. sp., larvae: 1. Labrum (left, dorsal view; right, ventral view). 2. Detail of brushlike setae on dorsal surface of labrum. 3. Detail of transverse row of setae on ventral surface of labrum. 4. Hypopharynx (right half). 5. Right mandible. 6. Left mandible. 7. Maxilla. 8. Labium. **Fig. 9.** *Hyrtanella christineae*, larva: Detail of labial palp.



FIGURES 10–14. *Hyrtanella pascalae*, n. sp., larvae: Fig 10. Foreleg. Fig. 11. Detail of apex of tibia. Fig. 12. Detail of foreclaw. Fig. 13. Middle femur. Fig. 14. Hind femur.

Male Subimago (Figs. 15–18)—Length: body (excluding caudal filaments) 5.5 mm; forewing 5.0 mm; hindwing 0.9 mm.



FIGURES 15–18. *Hyrtanella pascalae*, n. sp., male subimago: 15 Photograph of specimen in alcohol. 16. Forewing. 17. Hindwing. 18. Genitalia, ventral view.

Head: Vertex yellow-brown; antennae with scape and pedicel light yellow, flagellar segments light brown. Ocelli light yellow; median ocellus tinted with grey on posterior margin and lateral ocelli tinted with grey on inner margin. Compound eye with upper part yellow, lower part black.

Thorax: Prothorax brown with purple band on proximal margin. Mesoscutellum yellow-brown with light yellow maculae. Mesosterna light yellow with purple narrow longitudinal band medially. Legs yellow-brown, with tarsi pale; each leg with claws dissimilar (one blunt and paddlelike and one hooklike). Forewing (Figs. 15, 16) brown, with dark brown basally in subcostal field; few crossveins, mainly in radial and median fields; posterior margin with some irregular intercalaries; one intercalary between IMP and MP₂, and one between MP₂ and CuA; 3 intercalaries between CuA and CuP. Axillary cords (plumidia) long. Hindwing (Figs. 15, 17) brown with dark brown basally in subcostal and radial fields; crossveins absent; costa with well-developed process at middle; tip of process angled away from wing base.

Abdomen: Terga 1–3 and 8–10 yellow; terga 4–7 light brown; each with thin black band on anterior and posterior margins. Tergum 3 with pair of brown spots. Sterna brown, but with sterna 8 and 9 yellow. Gill socket vestiges on segments 3–7, decreasing in size posteriorly. Genitalia (Fig. 18) with posterior margin of subgenital plate convex; forceps three-segmented; forceps segment 3 elongate. Penes fused and compact, with small median incision; outer, lateral margins subparallel distally and concave proximally. Caudal filaments broken and missing.

Female Subimago—Unknown.

Adults—Unknown.

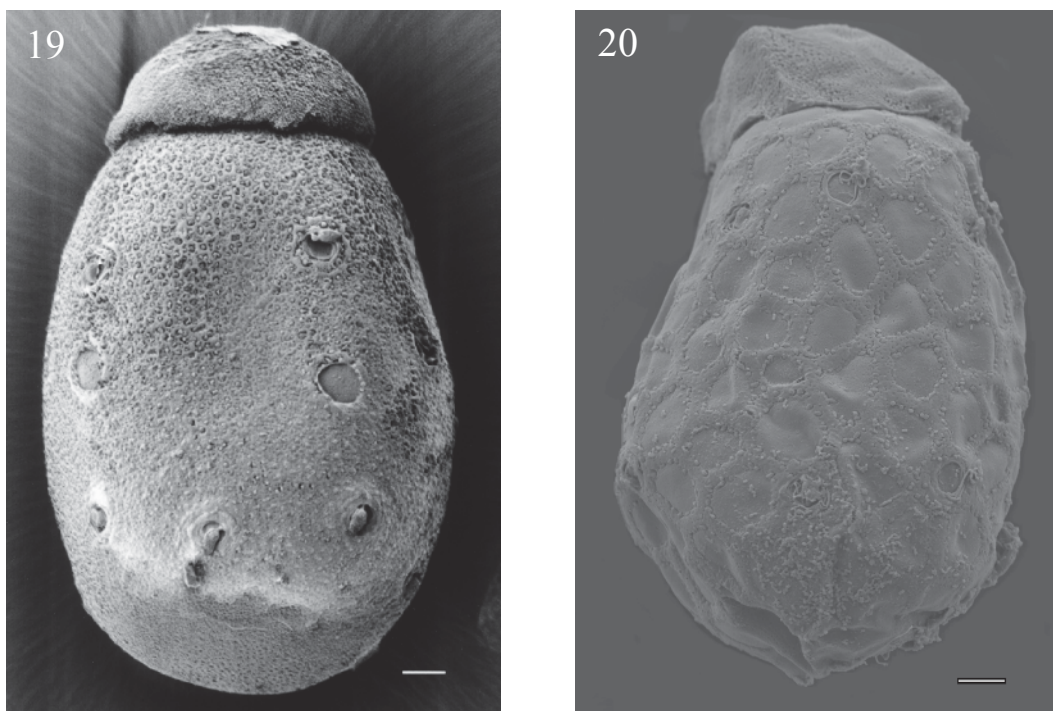
Egg (Fig. 19)—shape ovoid; one polar cap; chorion generally smooth, without reticulations; micropyles in equatorial position; large KCTs between equator and poles.

Diagnosis. *Larvae* of *H. pascalae* differ from those of *H. christineae* by being much smaller and by having bluntly expanded genae, no basal projections on the mandibles, the third segment of the labial palp (Fig. 8) more slender than that of *H. christineae* (Fig. 9), no dorsal projections on the upper surface of the forefemur, and no ventral projections on the thoracic and abdominal sterna.

Male subimagos (Fig. 15) of *H. pascalae* differ from *Hyrtanella* female adults beyond the usual sexual differences by having an abdomen that is not constricted, one small intercalary between MP₂ and CuA (Fig. 16), and the costal process of the hindwing with the tip angled away from the body (Fig. 17).

Male adults very likely have genital forceps segment 3 much longer than wide and penes lobes that are compact and nearly fused. This probable diagnosis is based on our examination of the male subimago.

Etymology. This species is named in honor of Dr. Pascale Derleth (Swiss Federal Institute of Technology, Lausanne), who collected much of the type material.



FIGURES 19–20. Eggs (scale bars = 10 μ m): 19. *Hyrtanella pascalae*, n. sp. 20. Undetermined Ephemerellinae, West Malaysia.

Larval variability. General color patterns vary from the typical light brown to dark brown. This variation appears to be between populations, and it is not dependent on the instar number. The number, relative development, and placement of chalazae on the ventral edge of the femora varies slightly between populations.

Ecology. *Hyrtanella pascalae* was collected commonly in the study areas of Indonesia, and sometimes it was locally abundant. It was sampled from stream riffles and runs with different substrate compositions, including silt, gravel, cobble, and boulders. Flow velocity at these sites ranged from 0.2–2.0 m/s; water depth was between 0.3–3.0 m; and at least some sites had a moderate silt load. Water temperature during the sampling period varied from 24.1°–26.4°C (Derleth 2003; Danuta Zaranko, pers. comm.). Multivariate analyses have shown that *H. pascalae* is more abundant in larger streams, and its distribution is positively correlated with the opening of the canopy, stream width, and water temperature (Derleth 2003). With respect to the influence of logging activities in the area, *H. pascalae* is characterised by population density increasing during, and until six months after, logging. However, the population density decreases one to three years after logging activity (Derleth 2003).

All localities where *H. pascalae* has been collected are situated between 100 and 400 meters above sea level, whereas collecting locales of *H. christineae* in Sabah are located between 900 and 1600 m. These species may represent altitudinal vicariants.

Material examined. Holotype: Island of Borneo—INDONESIA, **East Kalimantan:** Malinau Basin—*Seturan River tributary*: Temalat (Sungai Guang) trib., Loc. Seturan (2000-petak 43), 2°59'29" N, 116°33'29" E, 18/VI/2000, P Derleth, J-L Gattolliat, (B0811), 1 female larva [MZL].

Paratypes: *same locale and date*, 11 larvae [MZL]; same locale, but 16/VIII/2000, P Derleth, R Schlaepfer, (B0812), two larvae [MZL]; same locale, but 16/IV/2001, P Derleth, (B0813) one larva [MZL]; *other Seturan River tributaries*: Tamalang trib., Loc. Seturan (2001-petak 57), 2°59'22"N, 116°30'29" E, 18/VII/2000, P Derleth, F Béboux, (B0511), two larvae [MZL]; Tamalang trib., Loc. Seturan (2001-petak 57), 2°59'22"N, 116°30'46" E, 10/IV/2001, P Derleth, (B0513), 16 larvae [MZL]; Tamalang trib., Loc. Seturan (2001-petak 57), 2°59'50"N, 116°30'29" E, 19/VII/2000, P Derleth, F Béboux, (B0521), 14 larvae [MZL]; same locale, but 5/VIII/2000, P Derleth, (B0521PLS), one male subimago [MZL]; Bengahau trib., Loc. Seturan (2001-petak 57), 2°59'22"N, 116°30'46"E, 8/VIII/2000, P Derleth, (B0531), five larvae [MZL]; same locale, but 11/IV/2001, P Derleth, B Feldmeyer, (B0533), seven larvae [MZL]; Bengahau trib., Loc. Seturan (2001-petak 57), 2°59'22"N, 116°30'46" E, 19/VIII/2000, P Derleth, R Schlaepfer (B0541), ten larvae [BMNH, FAMU, MZL]; Kipah trib., Loc. Seturan (1998-petak 28), 3°01'48" N, 116°29'48" E, 29/III/2001, P Derleth, (B0913), one larva [MZL]; Seturan riv., Loc. Seturan (unlogged), 3°00'05" N, 116°30'48" E, 28/III/2001, P Derleth, B Feldmeyer, (B1313), 50 larvae [MZL]; Riv. Seturan, Loc. Seturan, Aff. cours principal, 3°00'05"N, 116°30'48"E, 28/III/2001, P Derleth, B Feldmeyer, three larvae [PERC]; unnamed trib., Loc. Seturan (unlogged), 2°59'49" N, 116°31'22" E, 17/IV/2001, P Derleth, M Sartori, B Feldmeyer, (B1513), one larva [MZL]. *Rian River tributaries*: Belakau trib., Loc. Langap Sud (1997-petak 6), 3°04'04" N, 116°30'26" E, Alt. 100 m, 20/IV/2001, P Derleth, M Sartori, (B0113), one larva [MZL]; Ngayo trib., Loc. Langap Sud (1995), 3°01'48" N, 116°29'48" E, Alt. 160 m, 14/VI/2000, (B0410), seven larvae [LIPI, MZL]; same locale, but 8/VII/2000, P Derleth, (B0411), two larvae [MZL]; Ngayo trib., Loc. Langap Sud (1995), 3°04'56" N, 116°30'58" E, Alt. 160 m, 13/VII/2000, P Derleth, (B0431), four larvae [MZL].

Other Material (not paratypes):

Island of Borneo—INDONESIA, **East Kalimantan:** Kelinjau R., about 10km upstream of Atan R., at logging staging area above rapids, 0°45'N, 116°15'E, 23/I/1997, one larva [PERC]. Island of Borneo—MALAYSIA (east), **Sabah:** Liwagu R at bridge, Ranau, 335m elev., 11–16/VIII/1972, GF&CG Edmunds, WL&JG Peters, four larvae [PERC]; Mantukungan R, S of Poring Hot Springs Station, 365m elev., 12/VIII/1972, WL&JG Peters, five larvae [PERC]; Sungai Moyog (26°C), 3 mi E of Penampung, 27–29/IX/1978, GF&CH Edmunds, seven larvae [PERC]; Sungai Moyog at tributary 8 mi E of Penampung, 2/X/1978, GF&CH Edmunds, one larva (mouthparts on slide) [PERC]; Penompange River, Crocher National Park, 8/VIII/2003, M Whiting team, seven larvae [MZL].

Discussion. We recommend that *Hyrtanella* female alates should not be identified to species until adults are associated positively with both *H. christineae* and *H. pascalae*. Allen and Edmunds (1976) had described female adults for *H. christineae*, but the association was not based on rearing, and the size of those female adults is similar to what would be expected from *H. pascalae*, rather than the larger *H. christineae*. The adults described by Allen and Edmunds (1976) probably belong to the genus *Hyrtanella*, because they share with the larvae the shape and armature of the abdomen, which is unique among genera of the family Ephemerellidae (sensu Wang & McCafferty 2000).

Material examined. Island of Borneo—MALAYSIA (east), **Sabah**, Liwagu R, N of Kundassan, 915m, 16–17/VIII/1972, WL&JG Peters, 15 female adults [FAMU].

ACKNOWLEDGMENTS

George Edmunds (Salt Lake City, Utah), Heath Ogden (Provo, Utah), Jan Peters (Tallahassee, Florida), and Danuta Zaranko (Guelph, Ontario) provided specimens and data. Patrick McCafferty (West Lafayette, Indiana) reviewed a draft of the manuscript and provided some funds for a portion of these investigations. Jeff Webb (West Lafayette, Indiana) provided some helpful criticism. Figure 19 was taken at the Electronic Microscopy Center, Lausanne University, by Geneviève L'Eplattenier. Figure 20 was taken at the Life Science Microscopy Facility, Purdue University, with the assistance of Chia-Ping Huang, Debra Sherman, and Lu Sun (West Lafayette, Indiana). Fieldwork and collecting in East Kalimantan by MS was possible thanks to financial support from the ZIL (Swiss Center for International Agriculture) through a research fellow grant to P. Derleth. Additional funding for this study was provided in part by USEPA fellowship 91601701-0 to LMJ, and in part this material is based upon work supported under a National Science Foundation Graduate Research Fellowship to LMJ.

REFERENCES

- Allen, R.K. (1980) Geographic distribution and reclassification of the subfamily Ephemerellinae (Ephemeroptera: Ephemerellidae). In: Flannagan, J.F. & Marshall, E. (Ed) *Advances in Ephemeroptera Biology*, Plenum, New York, pp. 71–81.
- Allen, R.K. (1984) A new classification of the subfamily Ephemerellinae and the description of a new genus. *The Pan-Pacific Entomologist*, 60, 245–247.
- Allen, R.K. & Edmunds, G.F., Jr. (1976) *Hyrtanella*: a new genus of Ephemerellidae from Malaysia (Ephemeroptera). *The Pan-Pacific Entomologist*, 52, 133–137.
- Bishop, J.E. (1973) Limnology of a small Malayan river Sungai Gombak. *Monographiae Biologicae*, 22, 1–485. Dr. W. Junk, The Hague.
- Derleth, P. (2003) *Benthic macroinvertebrates and logging activities: a case study in a lowland*

- tropical forest in East Kalimantan (Indonesian Borneo). Ph. D. Thesis, Swiss Federal Institute of Technology, Lausanne, Switzerland.
- Edmunds, G.F., Jr. & Polhemus, D.A. (1990) Zoogeographical patterns among mayflies (Ephemeroptera) in the Malay Archipelago, with special reference to Celebes. In: Knight, W. J. & Holloway, J.D. (Ed) *Insects and the Rain Forests of South East Asia*, Royal Entomological Society, London, pp. 49–56.
- Jacobus, L.M. & McCafferty, W.P. (2003) Revisions to the genus *Crinitella* (Ephemeroptera: Ephemerellidae). *Journal of the New York Entomological Society*, 111, 48–50.
- Jacobus, L.M., Zhou, C.-F., & McCafferty, W.P. (2004) Revisionary contributions to the genus *Torleya*. *Journal of the New York Entomological Society*, 112, 153–175.
- Kang, S.-C. & Yang, C.-T. (1995) Ephemerellidae of Taiwan (Insecta, Ephemeroptera). *Bulletin of National Museum of Natural Science*, 5, 95–116.
- Kluge, N. (2004) *The Phylogenetic System of Ephemeroptera*, Kluwer, Dordrecht, The Netherlands, 442 pp.
- Landa, V. & Soldán, T. (1985) Phylogeny and higher classification of the order Ephemeroptera: a discussion from the comparative anatomical point of view. *Studie CSAV, Československa Akademie Véd*, Praha, Czechoslovakia, 121 pp.
- Landa, V., Soldán, T. & Edmunds, G.F., Jr. (1982) Comparative anatomy of larvae of the family Ephemerellidae (Ephemeroptera). *Acta Entomologica Bohemoslovica*, 79, 241–253.
- McCafferty, W.P. & Wang, T.-Q. (2000) Phylogenetic systematics of the major lineages of Pannote mayflies (Ephemeroptera: Pannota). *Transactions of the American Entomological Society*, 126, 9–101.
- Okazaki, H. (1984) Observation of the eggs of Japanese mayflies by scanning electron microscope. *Biology of Inland Waters*, 3, 19–27.
- Sartori, M., Derleth, P. & Gattolliat, J.-L. (2003) New data about the mayflies (Ephemeroptera) from Borneo. In: Gaino, E. (Ed) *Research Update on Ephemeroptera & Plecoptera*, Università di Perugia, Perugia, Italy, pp. 403–406.
- Sites, R.W., Wang, T.-Q., Permkam, S. & Hubbard, M.D. (2001) The mayfly genera (Ephemeroptera) of southern Thailand. *The Natural History Bulletin of the Siam Society*, 49, 243–268.
- Studemann, D. & Landolt, P. (1997) Eggs of Ephemerellidae (Ephemeroptera). In: Landolt, P. & Sartori, M. (Ed) *Ephemeroptera & Plecoptera: Biology—Ecology—Systematics*, MTL, Fribourg, Switzerland, pp. 362–371.
- Wang, T.-Q. & Sites, R.W. (1999) Description of a new species of *Crinitella* (Ephemeroptera: Ephemerellidae) from Thailand. *Journal of the New York Entomological Society*, 107, 73–77.